Taxonomic Characterization of Some Live-stem Inhabiting *Azteca* (Hymenoptera: Formicidae) in Costa Rica, with Special Reference to the Ants of *Cordia* (Boraginaceae) and *Triplaris* (Polygonaceae)

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Abstract.—In the morphological space defined by queen head length and head width, seven Costa Rican species or species complexes in the ant genus *Azteca* have relatively narrow, subrectangular heads (head length ≥ 1.3 times head width), and all of them share characteristic nesting behavior in live stems. These species and species complexes are taxonomically characterized, and queen and worker-based identification guides are provided. A subset of these species are common inhabitants of the specialized ant plants *Cordia alliodora* (Boraginaceae) and *Triplaris melaenodendron* (Polygonaceae). *Azteca longiceps* is an obligate inhabitant of *T. melaenodendron*, but is known only from two mid-elevation Pacific slope sites. In the Pacific lowlands *T. melaenodendron* is usually inhabited by either *A. beltii* or *Pseudomyrmex viduus*, two species that are not obligate inhabitants of particular ant plants, but instead may be found in a variety of different ant plant species. The *Azteca pittieri* complex contains the common obligate inhabitants of *Cordia alliodora*. A general description of ant community composition in *Cordia* and *Triplaris* ant plants, and discussion of 1) the adaptive significance of queen characters in *Azteca*, 2) problems of species definitions as revealed by this study, 3) possible mechanisms generating complex character distributions in the *A. pittieri* complex, and 4) the contrasting roles of regional faunas and global revisions are provided. Taxonomic changes are: *Azteca beltii* Emery 1893, **new stat.** [= *laeta* Wheeler 1934 **new syn.**, = *stolli* Forel 1912 **new syn.**]; *Azteca cordincola* Forel 1920, **new stat.**; *Azteca juruensis* Forel 1904, **new stat.**; *Azteca nigricans* Forel 1899, **new stat.**; *Azteca patruelis* Forel 1908, **new stat.**; *Azteca pittieri* Forel 1899 [= *emarginatisquamis* Forel 1920 **new syn.**]; *Azteca sapii* Forel 1912, **new stat.**

INTRODUCTION

Specialized ant-plant associations are a conspicuous feature of the tropics, and they have been a frequent subject of study in ecology and evolutionary biology (Beattie 1985, Davidson & McKey 1993, Hölldobler & Wilson 1990). Most of the conspicuous ant-plant associations involve communities of interacting species (Longino 1989a, 1991a, Ward 1991, Fiala *et al.* 1991, Davidson *et al.* 1991, Davidson & Fisher 1991, McKey 1991). Studies of these communities are hampered by a lack of basic taxonomy and natural history of the organisms involved. Lack of names and/or a confused state of names impedes effective communication of results. An inability to distinguish among species can lead to misinterpretation of field results and/or an underestimation of diversity in ant plant associations. Two ant-plant associations that have received little attention involve the plant genera *Cordia* and *Triplaris*. The last review of these associations was by Wheeler (1942), which contains a wealth of taxonomic and natural history data.

The genus *Cordia* occurs throughout the Neotropics, and two species, *C. nodosa* and *C. alliodora*, are specialized ant-plants (Wheeler 1942). Both species have pyriform cauline swellings at nodes where whorls of branches arise. These domatia are hollow and are usually inhabited by ants. *Cordia nodosa* is South American. *Cordia alliodora* is widespread in South America and also extends through Central

America to southern Mexico. In Costa Rica, *C. alliodora* is the only myrmecophytic *Cordia*. It is a very common tree in anthropogenic habitats, occurring along roadsides and in pastures. On the dry Pacific side, the trees are usually small and bushy, with crooked trunks. On the wet Atlantic side, the trees are tall and straight. It has the common name "laurel" and is considered a valuable timber tree (Opler & Janzen 1983).

Wheeler (1942) considered the following to be obligate inhabitants of *Cordia alliodora*: "*Azteca longiceps* and its subspecies, *A. pittieri* and its var. *emarginatisquamis*, *Pseudomyrma sericea* and its varieties *ita* and *cordiae*, and *Ps. alliodorae*." Wheeler misidentified the material he called *Pseudomyrmex ita* (Forel). True *ita* is a generalist inhabitant of dead twigs, and is occasionally found in *Acacia* thorns (Ward 1993). The material Wheeler identified as "*ita*" is close to or the same as *P. cordiae* (Forel) (Ward, pers. comm.), and is probably an obligate *Cordia* ant. *Pseudomyrmex alliodorae*, described by Wheeler from his study of *Cordia*, is a junior synonym of *P. elongatus* (Mayr), a common and generalized inhabitant of plant cavities (Ward 1989). In the Canal Zone of Panama, Wheeler encountered what he interpreted to be two species of *Azteca* that were specialized inhabitants of *Cordia*. He identified them as *A. longiceps* and *A. pittieri*. *Azteca longiceps* was the most abundant, occurring in 85% of the domatia. The species was previously known only from the type queen, collected in Costa Rica with no biological data, and he redescribed it based on abundant material from *C. alliodora*. His results have influenced subsequent identifications of *Cordia* ants as *A. longiceps* (e.g. Opler & Janzen 1993). As reported below, true *A. longiceps* is a *Triplaris melaenodendron* specialist known from two sites in Costa Rica, and Wheeler's two *C. alliodora* ants should be interpreted as members of the *A. pittieri* complex.

Triplaris contains at least 17 species throughout the Neotropics, all of which have hollow stems that are inhabited by ants (Brandbyge 1986, Wheeler 1942). The hollow stems are much like *Cecropia* or bamboo, with short cylindrical internodes separated by solid septa. In many parts of South America, *Triplaris* trees are dominated by the *Pseudomyrmex triplarinus* complex, a set of at least four species of obligate *Triplaris* ants (Ward 1991). *Triplaris melaenodendron* subsp. *melaenodendron* (sensu Brandbyge 1986; often identified as *T. americana* in earlier literature; referred to as *T. melaenodendron* in this paper) occurs from Mexico to southern Costa Rica, and is the only *Triplaris* species in Costa Rica. *Triplaris melaenodendron* is moderately abundant on the Pacific side of Costa Rica, where it most often occurs along streams in dry forest areas (pers. obs.).

Wheeler (1942) examined numerous specimens of what he called *Triplaris americana* in Panama, which I assume to be *T. cumingiana* based on Brandbyge's (1986) revision. Wheeler found two ant species he considered to be obligates: *Azteca menceps* and "*Pseudomyrma loewensohni*". *Azteca menceps* is not known from Costa Rica (pers. obs.). The material Wheeler identified as "*loewensohni*" (an unavailable name; Ward 1989) is *symbioticus*, an obligate *Triplaris* ant in the *P. triplarinus* complex, and known from Panama and northern South America (Ward, pers. comm.). As reported below, Costa Rican *T. melaenodendron* is inhabited by a somewhat less specialized community of ants, without close affinities to the specialist *Triplaris* ants from South America.

Ants in the dolichoderine genus *Azteca* are major elements of neotropical forest ant communities (Forel 1899). All are arboreal. The numerous species exhibit a variety of nesting habits, inhabiting external carton nests, dead branches, dead cores of living trees, and live branches. A number of species are obligate inhabitants of specialized ant plants (reviewed in Davidson & McKey 1993). Forel (1878) established

the genus, and his definition remains essentially unchanged. Shattuck (1992) recognized the genus as a monophyletic lineage within the Tapinomini. Emery (1893) provided the first and as yet only revision of *Azteca*, recognizing 25 valid names, but there are now over 150 available names (Shattuck 1994) due to subsequent disconnected descriptions. Longino (1989b, 1991b) has recently reviewed the taxonomy of the species that are obligate inhabitants of *Cecropia* trees.

My studies of the Costa Rican ant fauna have revealed at least 20 species of *Azteca* in the country. Seven of these species nest in live plant stems and have queens with relatively long, narrow heads (head length greater than or equal to 1.3 times head width). This report addresses the taxonomy and natural history of these seven species. The species treated here include the obligate inhabitants of *C. alliodora* and *T. melaenodendron*, as well as other less specialized inhabitants of a variety of plant species. The remaining known Costa Rican *Azteca*, including the five obligate *Cecropia* ants (Longino 1989b, 1991b), have queens with relatively broader heads (head length less than 1.3 times head width).

This is an intentionally regional work. Differentiating species within Costa Rica has proven difficult. Distinguishing continuous geographic variability from discontinuous character change is difficult even in an area the size of Costa Rica, and challenges species concepts. Thus, formal taxonomic changes are restricted to "nomenclatural housecleaning" for a few obvious cases. Species that are insufficiently well-known, primarily due to inadequate knowledge of character variation within and outside of Costa Rica, are given taxonomically unavailable code names. These code names are developed by the author and are unique within the genus *Azteca*. In the future, if numbered taxa are named or associated with existing available names, the numbers will be retired and not reused.

The term "complex" is used for clusters of phenetically similar organisms for which 1) the range of character variation is greater than that typically observed in single species, 2) character variation is at least partially discontinuous, suggesting multiple species, and 3) either the discontinuity is geographically unstable (e.g. *Azteca pittieri* complex) or there is insufficient material to evaluate its stability (e.g. *Azteca nigricans* complex).

A provisional taxonomy is provided, along with keys to queens and workers. The taxonomic results are based on queens because they show greater differentiation between species than workers or males (Longino 1991b, Wheeler and Bequaert 1929). Distinguishing species from workers alone is problematic, because workers exhibit continuous size polymorphism, and colonies of the same species vary greatly in the size of the largest workers. Following the species accounts are a summary of *Cordia* and *Triplaris* ant community composition in Costa Rica, and discussions of 1) the adaptive significance of queen characters, 2) problems of species definitions as revealed by this study, 3) possible mechanisms generating complex character distributions in the *A. pittieri* complex, and 4) the contrasting roles of regional faunas and global revisions.

LIVE-STEM NESTING *AZTECA*

All members of the group described here nest in live stems. When in *Cordia*, *Triplaris*, or *Cecropia* they inhabit pre-formed cavities in the stems. When in plant species without pre-formed cavities, they occupy irregular chambers throughout the stems, apparently excavated by the workers themselves. Only young stems are occupied; older parts of the plant are gradually abandoned. Colonies are usually polydomous, with all or large parts of a plant crown being inhabited. Brood, often including sexual brood or alate adults, is dispersed throughout the colony space. No cases of polygyny are known, and workers must transport brood among nests in a polydomous colony. Carton construction is common, usu-

ally in the form of small platforms and baffles inside the stems, but sometimes extending outside of the stems to form runways along the stem surfaces. The insides of the stems are usually packed with Homoptera (Coccoidea: mealy bugs and scales), and when carton galleries extend outside of the chambers, abundant Homoptera are often found underneath. Workers do not appear to forage off their host plant, and conspicuous patrolling or foraging outside of the stems is rarely observed. Thus, colonies of these species are relatively inconspicuous. Workers are often somewhat timid, emerging and biting only when the nest space is violently disturbed or actually broken open. A completely different ant fauna may occupy the outer surfaces of the host plant.

METHODS

Measurements were taken at 50× magnification, using a Nikon micrometer stage with an orthogonal pair of Boeckler rotary micrometers, wired to a dual-axis digital readout. The output of the measuring device was in 0.0001mm increments, and the raw data were recorded as such, but 10 replicate measurements of head length of one specimen had a standard deviation of 0.0025mm. Thus, the 95% confidence interval for measurements spans 0.003mm. Measurement definitions are in figure captions.

The following abbreviations of research collections are used:

IBCR: Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.

LACM: Los Angeles County Museum of Natural History, Los Angeles, CA, USA.

MCSN: Museo Civico di Storia Naturale "Giacomo Doria," Genoa, Italy.

MCZC: Museum of Comparative Zoology, Cambridge, MA, USA.

MHNG: Muséum d'Histoire Naturelle, Geneve, Switzerland.

The specimens examined in this work

were mainly from my research collection. These specimens will be deposited in research museums (primarily LACM and IBCR).

CHARACTERS

Species definitions are based on the following character set:

Queens

- Head shape (Fig. 1).
- Plot of head width vs. head length (Fig. 2, 3; measurement definitions provided in figure caption).
- Mandible sculpture and pilosity (Fig. 4).
- Pilosity of the propodeum (Fig. 5).
- Shape of the petiole in lateral view (Fig. 6).
- Color
- Plot of head width vs. scape length (Fig. 7).

Workers

- Head shape of largest workers (Fig. 8).
- Plot of head width vs. head length (Fig. 9).
- Plot of head width vs. scape length (Fig. 10).
- Pilosity of the mesosomal dorsum (Fig. 11).

Each character (except color) is illustrated, with a discussion in the caption of character variation. The figures and keys provide diagnostic information, so it is not repeated in species accounts. Species accounts contain taxonomic changes, taxonomic comments, distribution data, and biological data. Costa Rican place names are used commonly in the species accounts (Fig. 12).

TAXONOMIC SYNOPSIS

Azteca beltii Emery 1893, **new stat.**; Honduras to Panama; ant-plant generalist
    = *fasciata* subsp. *laeta* Wheeler 1942, **new syn.**
    = *stolli* Forel 1912, **new syn.**
Azteca cordincola Forel 1920, **new stat.**, Bolivia; *Cordia* specialist?

Azteca JTL-003, unavailable code name; Costa Rica; *Cordia* specialist

Azteca JTL-007, unavailable code name; Costa Rica; *Ocotea* specialist?

Azteca juruensis Forel 1904, **new stat.**, Brazil; in *Swartzia* stems (Fabaceae)

Azteca longiceps Emery 1893; Costa Rica; *Triplaris* specialist

Azteca nigricans Forel 1899, **new stat.**; Panama

Azteca (*nigricans* complex) JTL-001, unavailable code name; Costa Rica; live-stem generalist

Azteca (*nigricans* complex) JTL-002, unavailable code name; Costa Rica; live-stem generalist

Azteca patruelis Forel 1908, **new stat.**, Mexico (*pittieri* complex); *Cordia* specialist?

Azteca pittieri Forel 1899; Costa Rica; *Cordia* specialist

  = *pittieri* var. *emarginatisquamis* Forel 1920, **new syn.**

Azteca sapii Forel 1912, **new stat.**, Brazil; in *Sapium* stems (Euphorbiaceae)

KEY TO QUEENS

   Key to *Azteca* queens that: 1) are known to occur in Costa Rica, and 2) have subrectangular heads, with head length ≥ 1.3 times head width. Species definitions in this treatment strongly rely on length and width of the queen head capsule, and the key should be used in conjunction with Figures 2 and 3.

1.a. Color largely orange; head width > 1.2mm (Fig. 2) . . . .*beltii*
1.b. Color largely or entirely black; head width < 1.2mm 2
2.a. Mandible with even covering of coarse, piligerous puncta (Fig. 4A); mandible surface appearing bristly (*nigricans* complex) 3
2.b. Mandible always with row of piligerous puncta along masticatory margin, but large puncta sparse to absent on mandible surface proximal to this row, and with at most four puncta bearing setae (Fig. 4B-F) 4
3.a. Petiolar node low and blunt, ventral lobe deep (Fig. 6D); scape relatively short (Fig. 7) **JTL-001**
3.b. Petiolar node sharp; ventral lobe shallow (Fig. 6E); scape relatively long (Fig. 7) . . . **JTL-002**
4.a. Head strongly rectangular, with flat sides and lateral margin of vertex relatively sharp (Fig. 1, *longiceps* and JTL-003); head length > 0.275 + 1.3(head width) (above line in Fig. 2) 5
4.b. Head less rectangular, with sides slightly convex, and lateral margin of vertex more broadly rounded (Fig. 1, remaining species); head length < 0.275 + 1.3(head width) (below line in Fig. 2) 6
5.a. Petiolar node low, anterior face of petiole flat (Fig. 6C); propodeum with sparse short setae concentrated posterior to spiracle (Fig. 5C); mandible lacking large puncta proximal to masticatory margin (Fig. 4E) **JTL-003**
5.b. Petiolar node higher, anterior face somewhat concave (Fig. 6B); propodeum with setae sparse or abundant (Fig. 5); mandible with about 5 large puncta proximal to masticatory margin (Fig. 4F) . . . .*longiceps*
6.a. Mandible with about 5 large puncta proximal to masticatory margin, about 3 of these bearing setae (Fig. 4C); propodeum sparsely setose (Fig. 5C) **JTL-007**
6.b. Mandible with about 3 large puncta proximal to masticatory margin, these not bearing setae (Fig. 4D); propodeum densely setose over most of surface (Pacific slope; Fig. 5A) or sparsely setose (Atlantic slope, Fig. 5B) . . . . *pittieri* complex

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KEY TO WORKERS

   This key is a corroborative device when one also has queens and/or host plant data.

1.a. Promesonotum with sparse pilosity (Fig. 11A); setae present on propodeum; head width of largest workers often, but not always, > 1mm (Fig. 9) 2
1.b. Promesonotum with abundant pilosity (Fig. 11B-E); propodeum with or without pilosity; head width of largest workers often, but not always, < 1mm (Fig. 9) 3

2.a. Head and pronotum red or orange, grading to brown posteriorly, appearing bicolored
      in the field . . . .*beltii*
2.b. Color more uniform red brown **JTL-003**
3.a. Propodeum lacking or with at most one or two short erect setae (Fig. 11D,E); mandibles
      bristly (*nigricans* complex) 4
3.b. Propodeum with more than 5 conspicuous erect setae; mandibles with or without bristles
      5
4.a. Scapes relatively short (Fig. 10); mesosomal pilosity relatively long (Fig. 11E) **JTL-001**
4.b. Scapes relatively long (Fig. 10); mesosomal pilosity relatively short (Fig. 11F) **JTL-002**
5.a. Head relatively narrow (Fig. 9); inhabitants of *Triplaris melaenodendron* . . . .*longiceps*
5.b. Head relatively wider (Fig. 9); inhabitants of *Cordia alliodora* or *Ocotea nicaraguensis* 6
6.a. Common inhabitant of *Cordia alliodora* . . . .*pittieri* complex
6.b. Inhabitant of *Ocotea nicaraguensis*, known from one collection at Carara **JTL-007**

SPECIES ACCOUNTS

Azteca beltii Emery new stat.
(Figs 1–11)

Azteca bicolor race *beltii* Emery, 1893:142. Holo-
    type worker, Costa Rica (Alfaro) [MCSN]
    (examined).
Azteca fasciata subsp. *laeta* Wheeler, 1942:227.
    Holotype (unique syntype) queen: Panama,
    Canal Zone, Barro Colorado Island, 9 July
    1924 (Wheeler #637), from a domatium of
    Cordia alliodora [MCZC] (examined). **new
    syn.**
Azteca stolli Forel, 1912:54. Syntype workers:
    Guatemala, Retaluleu (Stoll) [MHNG] (ex-
    amined). **new syn.**

Under *beltii* Emery (1893) described a
major worker from one collection and two
small workers from a different collection.
In the publication he designated the single
major worker as the type (considered the
holotype here), and conjectured that the
smaller workers might represent a distinct
taxon. The major worker, collected by Al-
faro and simply labeled "Costa Rica,"
matches material commonly collected
from *Triplaris* and other trees in the Pacific
lowlands of Costa Rica. The smaller work-
ers, also examined, are from "Jimenez," a
lowland Atlantic site, and are workers of
Azteca alfari. The *stolli* syntype workers
clearly come from a single nest series, and
appear identical to queen associated ma-
terial of *beltii* from Costa Rica and Hon-
duras.

Large size, orange head, and sparse dor-
sal pilosity make workers of this species
relatively distinctive. *Azteca beltii* is known
to occur from Guatemala to Panama. In
Costa Rica it is common at Santa Rosa,
Palo Verde, and along the road to Mon-
teverde. It is one of the more common in-
habitants of *Triplaris melaenodendron*, but
has also been collected from *Cordia nodosa*,
Cecropia peltata, *Cochlospermum vitifolium*
(Janzen, pers. comm.), and *Pithecellobium
saman*. Colonies can be large, filling the
crown of large *Pithecellobium* trees. The
nest space is entirely within live stems at
branch tips, and workers are rarely seen
foraging outside of the stems. This species
is much more common than museum col-
lections might suggest, because of its cryp-
tic habits.

An observation of queen founding be-
havior is described below under *A. longi-
ceps*.

I have examined scattered material from
southern South America that is either the
same species, a close relative, or a highly
convergent species. These include the type
queens of Emery's *fasciata* and *mayri*, for-
mer syntype workers of *bicolor* (workers
excluded from types and *bicolor* synony-
mized with *alfari* in Longino 1991b), and
recent Bolivian collections by P. S. Ward.
If the South American material is *beltii*,
then the biology and distribution of *beltii*
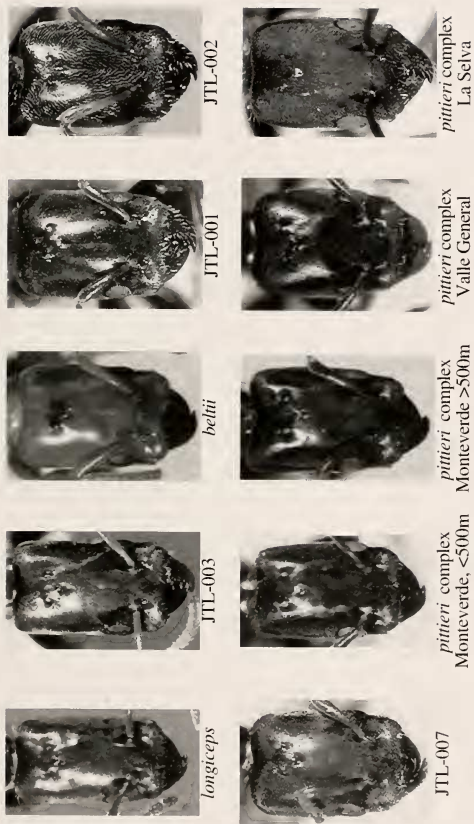is strikingly similar to that of *Pseudomyr-*

Fig. 1. Queen head shape. Image scales are adjusted to equalize head size in figure. For relative size data, see Figure 2.

mex viduus (Ward 1991). Both show catholicity with respect to which ant-plants they will inhabit, and both are present in both Central America and southern South America.

Azteca cordincola Forel new stat.

Azteca longiceps subsp. *cordincola* Forel, 1920: 203. Holotype (unique syntype) worker: Bolivia (Bang, n.1178) in cauline swellings of *Cordia* [MHNG] (examined).

The single small worker (head width 0.59mm) is nondescript and I cannot distinguish it from most *Azteca* species. Wheeler (1942:232) described the queen and redescribed the worker based on Mann collections from cauline swellings of *Cordia alliodora* in Ivon, Beni, and Huachi Beni, Bolivia. Wheeler also listed "Cochabamba" as the type locality for *cordincola*, although this does not appear in the original description nor on the type specimen label. The queen that Wheeler described has head length 2× head width, and so may be part of the *pittieri* complex, but Mann's collections cannot be assumed conspecific with the type.

Azteca JTL-003
(Figs 1–11)

This species is known only from between 400–500m on the road to Monteverde, from six different *Cordia alliodora* trees. It has been collected in two different clusters of trees along the road, and is sympatric with *A. beltii*, *A. longiceps*, and two forms of the *A. pittieri* complex.

Azteca JTL-007
(Figs 1–11)

This species is known from one collection from Carara Biological Reserve. *Ocotea nicaraguensis* is an understory lauraceous tree at Carara. It is part of a group of understory Lauraceae whose stems are always occupied by ants (Stout 1979, Hammel 1986, Burger & van der Werff 1990). The ants are usually obligate inhabitants in the genus *Myrmelachista*, but

Pseudomyrmex viduus and *Azteca* may also be found. During a brief examination of *O. nicaraguensis* plants at Carara, I observed that plants in shaded understory were small and all inhabited by *Myrmelachista*, while plants in more sunny areas along stream banks were larger and inhabited by *Azteca*. However, only one voucher collection of the *Azteca* was taken, from a vigorous colony with alate queens in the stems.

Azteca juruensis Forel new stat.

Azteca longiceps var. *juruensis* Forel, 1904:699. Syntype workers, females, male(s): Brazil, Amazonas, Jurua, Jurua Mirim, Aug 1901 (Ule), in branches of *Schwartzia* [MHNG] (examined).

A syntype queen has head length 1.24mm, head width 0.77mm. In general habitus *juruensis* looks like a *pittieri* complex species, including the same lateral profile of the petiole. The size is considerably smaller than any Costa Rican material. It is very similar and possibly conspecific with *sapii* (see below). I cannot distinguish the two, but I defer synonymy for lack of data on character variation in Amazonian stem-nesting *Azteca*.

Azteca longiceps Emery 1893
(Figs 1–11)

Azteca longiceps Emery, 1893:344. Holotype (unique syntype) queen: Costa Rica, Alajuela (Alfaro) [MCSN] (examined).

The species is now known from the type queen, collected in Alajuela before the turn of the century, and seven collections, all from between 700 and 900m elevation in the Guacimal river valley below Monteverde. The type has no biological data. The seven new collections are all from live stems of *Triplaris melaenodendron*. Some collections are from mature colonies, and others are founding queens from stump sprouts. Extensive collections in the area have not revealed *longiceps* using any oth-
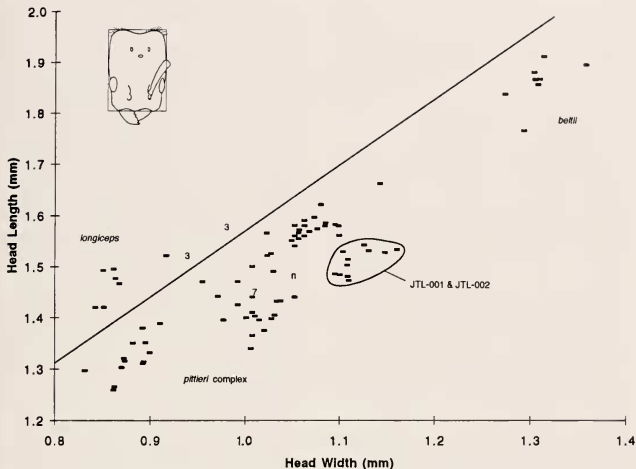
Fig. 2. Queen head width vs head length. Head width is the greatest width of the head in full-face view. Head length is measured along the median axis, from the anterior border of the clypeus to a line tangent to the posteriormost extent of the vertex lobes. Line: Head Length = 0.275 + 1.3(Head Width). "n" = nigricans type; "3" = JTL-003; "7" = JTL-007.

er plant species, and so *longiceps* is probably a host specialist in *T. melaenodendron*.

The discovery of *longiceps* as a *Triplaris* ant was unexpected. Subsequent to the naming of *longiceps*, Forel named a number of *longiceps* subspecies based on ants from *Cordia* and other plants (*cordincola*, *patruelis*, *juruensis*, and *sapii*). Wheeler (1942) encountered two species of *Azteca* regularly inhabiting *Cordia alliodora* in Panama (Canal Zone). He identified the more common one as *longiceps*, and thoroughly described the worker, queen, and male based on his new material. Myself and other contemporary workers have continued to identify the common *Cordia* ants as *longiceps* or cf. *longiceps*. Examination of the type revealed that *longiceps* was not one of the common *Cordia* ants. Short-

ly after examination of the type, the Monteverde population of *longiceps* was discovered in *Triplaris* trees. As interpreted here, *longiceps* is a narrowly circumscribed *Triplaris* ant, with the queen head relatively narrower than most *Cordia* ants. The *Cordia* ants examined by Wheeler are interpreted here as more closely related to *pittieri* than to *longiceps*, all are raised to species elsewhere in this paper. In order to dissociate the infraspecific taxa *cordincola*, *patruelis*, *juruensis*, and *sapii* from *longiceps*, all are raised to species elsewhere in this paper.

The following observations, derived from field notes, describe the nesting habits of *A. longiceps*:

5 July 1991, Longino #2956: I climbed a *Triplaris* tree and cut out 3 small branches that all contained parts of a colony. No workers appeared as I climbed the tree,

nor after I cut branches. A few workers emerged from cut branch bases. Only as I began to split stems did large numbers of workers swarm out. Abundant Homoptera were inside stems, and a few males and a few alate queens. There was abundant worker brood throughout.

I examined a 24cm long section in detail. The internodes contained "knöllen," discrete mounds of sticky bran-like material filled with nematodes, tiny dipteran larvae, and what appeared to be abundant stylets of Homoptera. (Knöllen are also found in nests of Cecropia ants (Müller 1880–1881, Longino 1991a), and are probably common to many or all stem-nesting Azteca.) There were pink coccids in the occupied internodes: 5, 7, 32, 31, 8, 7, 4 coccids in the 7 occupied internodes. There was a single pseudococcid in these 7 internodes. Many of the exit holes were originally large enough to accommodate a queen, but had been reduced to worker size with resinous carton. Some of the internodal septa were perforated, others not. There were perforated partitions made of resinous carton, which formed artificial septa. Some were found in the middle of internodes, others were partially closing chewed-out internodal septa.

There was one unoccupied internode in the middle of the branch, with solid septa on both sides. The sclerenchyma was thicker on the occupied side than the unoccupied side of the septa, as though the sclerenchyma were a secondary response to ant presence. The walls of ant-occupied internodes were black. The walls of unoccupied internodes were covered with flaky red brown material. Inner diameters of occupied internodes were greater than inner diameters of unoccupied internodes, but the sclerenchyma layer was thicker in the former, again suggesting that the sclerenchyma layer was a response to the ants.

The ant entrance holes were irregularly scattered, not in any predictable location. The terminal internodes, near the unoc-cupied apical shoot area, were the most recently entered.

5 July 1991, Longino #2972: I climbed a 4m tall Triplaris tree. It contained a populous colony, and workers emerged onto trunk when I climbed tree. The largest branch segments I examined from this tree were 3cm dia., and still contained hollow internodes with ants. A large basal section contained relatively few workers and scattered pseudococcids, with no coccids. Exit holes were still maintained through 1cm of wood. I dissected 180cm of occupied branch. There were abundant brood, workers, carton partitions, and exit holes, much like #2956. There were scattered alate queens, and at least one male. Unlike #2956, there was no trace of pink coccids, and pseudococcids were widespread and common.

5 July 1991, Longino #2969-s: I cut one branch from a Triplaris tree. The terminal 20–40cm, the leafy part, was unoccupied. Lower in the branch, 2 founding queens of Azteca longiceps and beltii occupied adjacent cavities. The cavities of the two queens formerly were continuous through a perforated septum, but a plug of particulate matter separated the two. The plug was asymmetrical, as though built from the beltii side (Fig. 13).

Azteca nigricans complex

The queens of this complex have the mandibles with an even cover of large piligerous puncta, so that the mandibles are bristly. Azteca nigricans s.s. is known only from the type queen from Panama, JTL-001 occurs in the Pacific lowlands of Costa Rica, and JTL-002 occurs in the Atlantic lowlands. The three "species" recognized here differ in queen head size and relative scape length. However, samples are available from few localities, and knowledge of geographic variation in these characters is inadequate to confidently establish species boundaries.
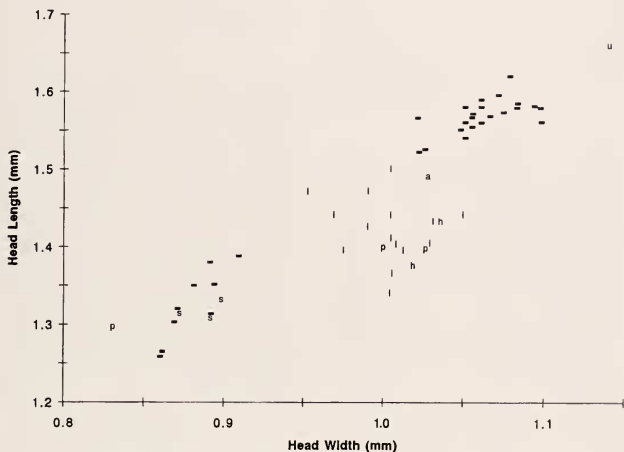
Fig. 3. Queen head width vs head length for *Azteca pittieri* complex. Dashes = road from PanAmerican Highway to Monteverde; "a" = Nuevo Arenal, on north side of Lake Arenal; "h" = Hone Creek, south of Limón; "l" = La Selva; "p" = 4–10km east of Palmar Norte, along the Río Grande de Térraba; "s" = Santa Rosa National Park and vicinity; "u" = Santiago de Puriscal.

Azteca nigricans Forel, new stat.

Azteca fasciata var. *nigricans* Forel, 1899:122. Unique syntype queen: Panama, Bugaba, Volcan de Chiriqui (Champion) [MHNG] (examined).

Azteca (nigricans complex) JTL-001
(Figs 1–11)

This species is known from a number of nest collections from lowland rainforest in southwestern Costa Rica, and two alate queens in collections: one from Golfito, and one from Cerro el Hacha near Santa Rosa.

The following observations, derived from field notes, describe the nesting habits of this species:

28 Aug 1982, Longino #28Aug82/1500: In the uppermost crown area of a large *Licania* tree (Chrysobalanaceae), a colony occupied chambers in the center of nearly every branch tip I could reach. The chambers looked chewed out by ants, and were not a natural feature of the plant. The chambers had many pink coccids on the walls, and some chambers had brood. The branches showed a history of synchronous new growth flushes. Chambers in the latest flush were most active; chambers in older or dead stems were abandoned or had few workers. The chambers in sequential shoots were usually not connected. All the chambers were connected externally by an extensive system of galleries, made of a black, very crusty carton, filled with tiny, circular holes.

3 Sep 1982, Longino #3Sep82/1100: In the same canopy *Licania*, I observed a queen investigating a small hole in a living shoot. The hole was too small for her to enter.

25 Mar 1990, Longino #2651: A colony occurred in live stems of a small *Grias* tree (Lecythidaceae). Branch surfaces were covered with black, crusty carton, with a high density of small, circular entrance holes. Irregular cavities in stems contained abundant Homoptera.

28 Sep 1982 (Longino): Founding queens were in separate chambers at the tips of living branches, 10m high in a tree (Moraceae). The stems of this tree frequently had small, pre-formed internal chambers, some with dead *Azteca* remains.

Leeanne Tennant studied the ant-plant *Tetrathylacium costaricensis* (Flacourtiaceae) in Corcovado National Park, during July 1987. She found JTL-001 to be one of the most common inhabitants. This ant-plant has pre-formed chambers that split, allowing entrance of ants without excavation.

Azteca (nigricans complex) JTL-002

This species is known from numerous recent collections from La Selva Biological Station, and one old (1926) collection from Parismina, on the Atlantic coast. Like JTL-001, it appears to be a generalist, nesting in live stems of a variety of plant species. At La Selva, workers were encountered in two of 18 canopy fogging samples, from crowns of *Carapa guianensis* (Meliaceae) and *Tapirira guianensis* (Anacardiaceae). Nests have also been sampled from scattered small chambers in live stems of *Dendropanax arboreus* (Araliaceae), *Pentaclethra macroloba* (Leguminosae), *Inga* sp. (Leguminosae), *Erythrina peoppigiana* (an introduced species, Leguminosae), and *Phoebe chavarriana* (Lauraceae). Wetterer collected a founding queen in an internode of a *Cecropia insignis* sapling. Although inconspicuous, *Azteca* JTL-002 is one of the most common *Azteca* species in the canopy at La Selva.

Azteca patruelis Forel, new stat.

Azteca longiceps subsp. *patruelis* Forel, 1908:392. Syntype workers, queen: Mexico, near Coli-

ma (Townsend), in *Cordia alliodora* [MHNG] (examined).

A syntype queen of *patruelis* has head length 1.62mm, head width 1.10mm. In most characters, including head shape, it closely matches *pittieri* complex specimens from upper elevation collections near Monteverde (see below). Although not examined on the type, a queen from near the type locality (Mexico, Jalisco: Estación Biológica Chamela, 19°30'N, 105°02'W, 100m (Ward #9253), ex *Cordia alliodora*) differs slightly in the pilosity of the ventral surface of the petiole. On Costa Rican specimens, the setae on the anteroventral margin are longer and more appressed. Pending additional data on character variation between Costa Rica and Mexico, *patruelis* is retained as a valid species (see Discussion below).

Azteca pittieri complex
(Figs 1–11)

Ants in the *Azteca pittieri* complex are the primary obligate inhabitants of *C. alliodora* throughout Costa Rica. In some areas character variation is discontinuous, suggesting discrete, parapatric species, but these differences are not stable geographically. In a plot of queen head length vs. head width (Fig. 3), specimens from the Pacific lowlands form one cluster, specimens from above 500m near Monteverde form a second cluster, and specimens from the Atlantic lowlands and the Valle General form a third cluster somewhat intermediate between the first two. One queen from Santiago de Puriscal (swept from vegetation, and thus not known with certainty to be a *C. alliodora* ant) is discontinuously larger than all other queens examined.

Collections along an elevational transect (400–900m along the road from the Pan American Highway to Monteverde) revealed two phenotypes that could be interpreted locally as two species. One form has relatively small queens (Fig. 3), and
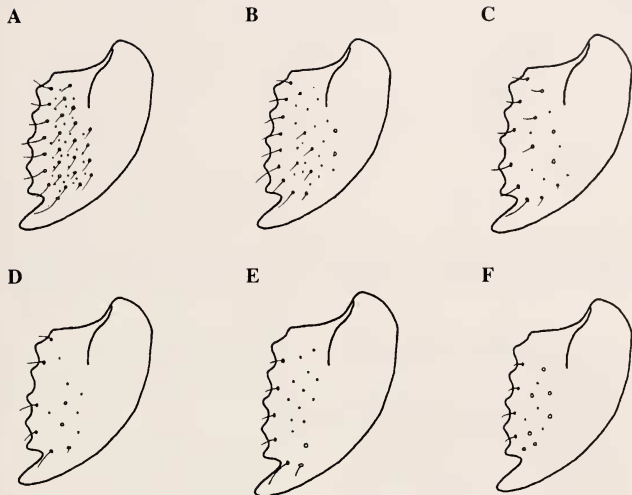
Fig. 4. Queen mandible sculpture and pilosity. A. *nigricans*, JTL-001, JTL-002; B. *beltii*; C. JTL-007; D. *pittieri* complex; E. JTL-003; F. *longiceps*.

workers with the margin of the vertex shallowly excavated and the sides of the head nearly flat (Fig. 8). The other form has relatively large queens, and workers with the margin of the vertex more deeply excavated and the sides of the head more convex. The two forms have a sharply parapatric distribution, with small-queen colonies occurring from 400–500m, and large-queen colonies occurring from 500–900m. In the narrow zone of sympatry both forms were found in adjacent trees, and founding queens of both forms were found in different nodes of the same small stump sprout or sapling. A similar pattern may occur on the more southern Pacific slopes, where one small and two large queens were collected near Palmar Norte (Fig. 3).

Variation in queen propodeal pilosity is discordant with head shape. Queens from the Pacific side of Costa Rica, regardless of queen head shape, have dense pilosity on the propodeum (Fig. 5A). Queens from La Selva on the Atlantic slope have sparser propodeal pilosity, and it varies from a uniform covering to a discontinuous covering, with a few setae near the mesopropodeal suture, a gap with no setae, and a cluster of setae posterior to the spiracle (Fig. 5B). La Selva queens with the relatively shortest heads are indistinguishable from two queens collected from Hone Creek south of Limón, and these relatively small queens exhibit the extreme of propodeal pilosity reduction. Relatively larger queens tend to have more uniform propodeal pilosity.

A   B   C
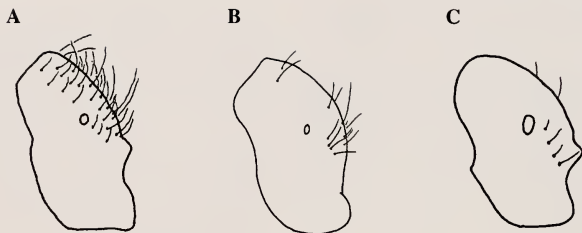
Fig. 5. Queen propodeum pilosity. A. Pacific slope *pittieri* complex. B. Atlantic slope *pittieri* complex. C. JTL-003, JTL-007, JTL-001, and JTL-002. *beltii* and *longiceps* are variable, with sparse setae that are either clustered posterior to the spiracle, as in **B**, or more uniformly distributed over the propodeum, but never dense as in **A**.

Azteca pittieri Forel

Azteca pittieri Forel, 1899:120. Syntype workers: Costa Rica, Buenos Aires (Pittier) [MHNG] (examined).

Azteca pittieri var. *emarginatisquamis* Forel, 1920: 204. Syntype workers: Costa Rica (Pittier, n.6701), found by Chodat in cauline swellings of *Cordia gerascanthus* [MHNG] (examined). **New syn.**

I examined an herbarium sheet at the National Museum of Costa Rica. It was part of the Pittier collection, and had the label "Cordia gerascanthus, arbre, Plaine du Rio Ceibo à Buenos Aires, Alt: 300m, Dat: I 1892, Legit: Tonduz," and it had Tonduz collection number 6701. It had a 1984 J. S. Miller determination label as *Cordia alliodora*. This collection was no doubt the source of the syntypes of *emarginatisquamis*, which Chodat probably found in a duplicate specimen in Europe. Thus *pittieri* and *emarginatisquamis* have the same type locality, and the types are possibly from the same colony. Pittier apparently distributed Tonduz collections under his own name (L. D. Gomez, pers. comm.), and thus the types of *pittieri* s.s. could have been from the same collection, sent to Forel by Pittier.

Azteca sapii Forel new stat.

Azteca longiceps race *sapii* Forel, 1912:56. Syntype workers, queens: Brazil, Amazonas, St.

Antonio de Iça (Ducke), in stems *Sapium glandulosum* [MHNG] (examined).

A syntype queen has head length 1.20mm, head width 0.73mm. I cannot distinguish this species from *juruensis* (see above).

COMMUNITY COMPOSITION AND DISTRIBUTION

Cordia alliodora

Individual *Cordia* trees usually harbor a number of ant species. In small saplings or stump sprouts, many species of founding queens may be found dispersed in the available nodes. In mature trees, live nodes typically house species distinct from those housed in dead nodes. Most often a dominant colony occupies most but not all of the live nodes, with smaller colonies of other species occupying the remaining nodes. Alternatively, a single dominant colony may not be recognizable. Instead, the tree may contain a mosaic of numerous colonies, or many nodes may be unoccupied.

The species of ants in individual trees are a subset of the surrounding community of available ant species. As with insect herbivores, those species exhibit a broad range of host specificity. A large number of species of generalist inhabitants of dead stems may be available to
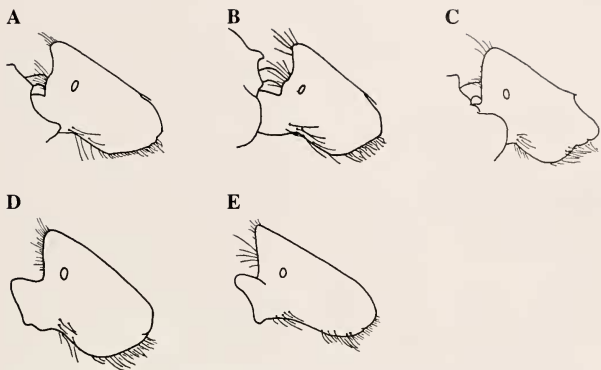
Fig. 6. Queen petiole shape and pilosity. Drawing scales are adjusted to equalize petiole size in figure. A. *beltii*. B. *pittieri* complex (JTL-007 and *longiceps* are the same). C. JTL-003. D. JTL-001. E. JTL-002.

occupy dead nodes of a *C. alliodora* tree. In the Neotropics these include members of the genera *Crematogaster*, *Dolichoderus*, *Tapinoma*, *Camponotus*, *Leptothorax*, *Pseudomyrmex*, *Brachymyrmex*, *Zacryptocerus*, *Paratrechina*, and others. A smaller number of generalist inhabitants of live stems may be available to occupy live nodes, and part or all of a crown may be inhabited by one or more colonies of these generalists. These include some species of *Crematogaster*, *Pseudomyrmex*, *Zacryptocerus*, and *Azteca*. These live stem generalists may have small colonies in one or a few nodes, or they may form large, dominant colonies that occupy much of the tree. Generalist inhabitants of *C. alliodora* show no obvious specialization for use of the plant. They are often scavengers and omnivores, and forage both on and off the plant. Species that form large, dominant colonies are not necessarily restricted to a single tree. Their large, polydomous colonies may extend into the surrounding vegetation.

In contrast to these generalists, a smaller

pool of available colonists make specialized use of *C. alliodora*. They usually form large, dominant colonies, occupying most or all of a live crown, and they are typically the most common inhabitants in an area. Their nest space is entirely within a single tree (or tight cluster of trees if from stump sprouts), and they do not forage off the tree. In spite of their local abundance in *C. alliodora* trees, they are never found nesting elsewhere, which suggests that they are obligate host specialists. The *Azteca pittieri* complex and, at least locally, *Azteca* JTL-003 appear to be the dominant or primary host specialists in Costa Rica.

Not all host specialists are dominant ants. The most ubiquitous inhabitant of *C. alliodora* is *Zacryptocerus setulifer* (Emery). This myrmicine ant has phragmotic soldiers which plug the entrance to the nest with their perfectly circular heads. They are inconspicuous and timid ants. They are capable of coexisting in the same tree with any of the above dominant ants, and they can live in trees without a dominant ant colony. They appear to be an obligate
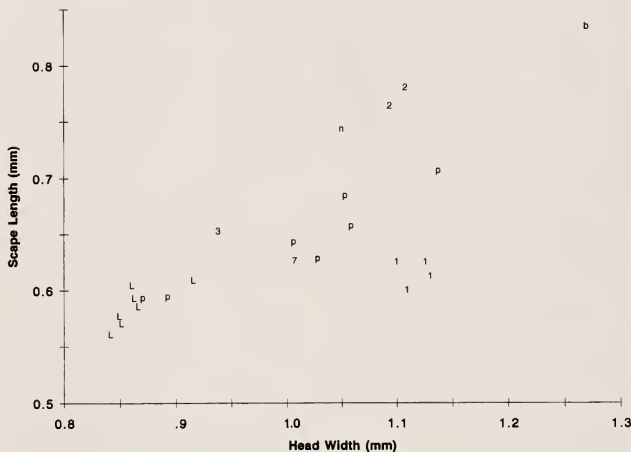
Fig. 7. Queen head width vs. scape length. "b" = *beltii*; "L" = *longiceps*; "n" = *nigricans* type; "p" = *pittieri* complex; "1" = JTL-001; "2" = JTL-002; "3" = JTL-003; "7" = JTL-007.

inhabitant of *C. alliodora*; I have never encountered them anywhere else. Nearly every *C. alliodora* population I have examined in Costa Rica has had *Z. setulifer* in some of the nodes.

Two ant species, *Pseudomyrmex viduus* (Fr. Smith) and *Azteca beltii*, show a combination of traits of host specialists and host generalists. They exhibit the behavior of a specialized plant-ant: they confine their nesting and foraging territory to the host tree itself, and, in the case of *P. viduus*, they may aggressively defend their host tree. However, they are generalists with respect to which species of host plant they inhabit. Both species can be found in different genera of well-known ant-plants (*e.g.*, *Cecropia*, *Triplaris*, and *Cordia*), and *A. beltii* has also been found in other species of non-ant-plants.

Most trees in populations of *C. alliodora*

are occupied by members of the *A. pittieri* complex, with *Zacryptocerus setulifer*, *Azteca beltii*, and *Pseudomyrmex viduus* as less common background elements. This is well-illustrated with data from an elevational transect. The road from the Pan-American Highway to Monteverde passes through an elevational gradient from 200m to 1400m, all of which is in pastures and second growth vegetation. *Cordia alliodora* trees are common in patches along the roadside, starting at 400m around Guacimal, and extending to about 900m, along 10km of road. In 1984 and in 1991, I sampled ants from *C. alliodora* trees along this road. *Azteca beltii* occurred occasionally throughout the transect. *Pseudomyrmex viduus* occupied patches of trees near 500m. I found *Azteca* JTL-003 in two patches of trees around 500m, and collected the only known samples of this species. Mem-

bers of the *A. pittieri* complex occupied the great majority of trees. As described earlier, there appeared to be two different biological species in the *A. pittieri* complex along this transect, with a lowland form changing to an upland form around 500m elevation.

It is unknown what impact parasitoids may have on community dynamics and structure. Founding *A. pittieri* complex queens are often attacked by parasitoid larvae inside *Cordia* nodes. They are probably larvae of *Conoaxima* (Eurytomidae); they are similar to larvae of *Conoaxima* I have observed attacking *Azteca* queens in *Cecropia* (Longino 1991b). At La Selva Biological Station I have observed larvae feeding externally on dead queens, and in two cases parasitoid pupae were on the walls with dead queen remains in the bottom.

Triplaris melaenodendron

Similar to *C. alliodora*, individual *T. melaenodendron* trees usually host a community of ants, and the same general observations regarding host generalists and host specialists apply. Dead branches and some live branches may be occupied by generalist arboreal ants, while the bulk of the live crown may be occupied by a dominant ant.

In contrast to the situation for *C. alliodora*, *T. melaenodendron* does not have a dominant host specialist ant in all parts of its range in Costa Rica. *Pseudomyrmex viduus* is the most common occupant in the Pacific lowlands, followed by *Azteca beltii*.

A dominant host specialist occurs near Monteverde. Along the road to Monteverde, between 700 and 900m elevation, *T. melaenodendron* occurs in a few spots along the road where there are seeps or stream crossings. *T. melaenodendron* trees also occur along the margins of the Río Guacimal (just below Monteverde on the Pacific slope), between 800 and 1000m. In 1991, I examined these trees, both along the road and along the Río Guacimal. In contrast to the lowlands, the most common inhabi-

tant was the specialist *A. longiceps,* followed in frequency by *A. beltii.* I found no *Pseudomyrmex viduus* at this elevation.

DISCUSSION

Adaptive Significance of Queen Characters

The species of live-stem inhabiting *Azteca* treated in this paper are often distinguishable by head size and shape, and by mandible sculpture and pilosity. Why should these characters vary between species, and have relatively low variance within species? And why are queens more differentiable among species than workers?

Alate queens of arboreal ant species must disperse and find suitable nest sites in vegetation. Ant queens are typically filled with flight muscles and reproductive organs, and thus are favored prey for birds, rodents, and other ants. While searching for nest sites, queens are highly conspicuous and vulnerable. There must be strong selection on queens to reduce this vulnerable period to a minimum. Selection should act to make queens extremely efficient at finding a particular kind of nest site, and quickly gaining access. Characters that influence nest site selection are concentrated in the head. Head size will influence the muscle mass available to power the mandibles, and thus will influence both the hardness of substrates that can be cut and the speed of cutting. Mandible sculpture and pilosity will also influence the performance of the mandibles on different substrates. Head size and shape will determine the size of stems that can be entered. Within species, selection may tailor head characteristics to optimally match a highly canalized behavioral (visual or chemical) search image for particular nest sites. Intense selection for specialization during colony founding may be driving diversification in *Azteca,* and this diversification is manifested in high interspecific diversity of queen head shape.
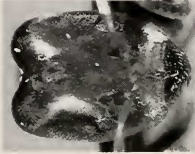
Fig. 8. Worker head shape. Image scales are adjusted to equalize head size in figure. For relative size data, see Figure 9.

The long, narrow heads of the species addressed in this paper may simultaneously provide great mandible strength and reduced head cross-section for entry into plant cavities in narrow stems.

Worker morphology may be much less constrained by nest site characters, and similarity between workers and queens may be the result of developmental constraints rather than strong selection on the workers. Strong selective factors acting on worker morphology are more likely to involve foraging and colony defense. These factors may vary little across *Azteca* species, and be independent of or only weakly influenced by nest site characters. Thus, there may be little selection for divergence in worker morphology between species.

Variation in queen mandible pilosity may also be strongly related to colony founding. The pilose mandibles of the *A. nigricans* complex are in striking contrast to the nearly hairless mandibles of the obligate *Cordia* and *Triplaris*-inhabiting species. Mandibles of *beltii* and JTL-007 exhibit intermediate degrees of pilosity. Differences in mandibular pilosity are not due to differential wear. Alate queens of *Cordia* and *Triplaris* ants that have yet to leave their natal nest have largely hairless mandibles, and the large puncta from which hairs arise would not be effaced by wear. *Azteca longiceps*, *pittieri* complex, and JTL-003 all appear to be primary occupants of specialized ant-plants. To found their colonies, they have to cut rapidly through plant tissue into a domatium. The smooth, hairless mandibles may be an adaptation for rapid cutting. *Azteca beltii* and JTL-007 have been found in ant-plants that have other primary occupants. Although there are no direct observations of founding behavior, the one observation of the close proximity of founding *longiceps* and *beltii* queens (Fig. 13) hints at the possibility that *beltii* and JTL-007 are secondary occupants of ant-plants. They may rely on the primary occupants to excavate entrances, entering subsequently and either

fighting or walling off the primary occupant.

The stiff setae on the mandibles of ants in the *A. nigricans* complex appear as though they would impede cutting into plant stems. In the case of *Tetrathylacium costaricensis*, it is clear that the queens do not have to excavate an entrance hole to enter the stems; on maturation the stems split down the side, allowing ant entry. Perhaps ants in the *A. nigricans* complex, rather than being specialized to excavate entrances in a particular kind of hostplant, are instead specialized to find preexisting entrance holes into plant cavities, regardless of plant species. Strongly pilose mandibles may be an adaptation for efficient and rapid construction of carton nest material, which would be necessary to close large and/or irregular preexisting entrances.

These speculations regarding the functional aspects of queen head morphology deserve greater study. Direct and close observations of early nest establishment behavior by *Azteca* queens are needed.

Problems of Species Definitions

The *A. pittieri* complex exhibits at least one area where two morphologically diagnosable groups of organisms are parapatric, with the zone of sympatry being less than 5km wide. However, the characters that are diagnostic in this area are not stable in other parts of the range. Taxonomists routinely face this level of knowledge about patterns of organismal diversity, and the frequency of encountering patterns such as this can only increase with the current emphasis on intensive biodiversity inventories at the national or more local scale (Janzen 1991, Longino 1994, Stork 1994). How taxonomists treat this situation nomenclaturally underlies the conflict that often occurs between the local field collector's and the museum taxonomist's definitions of species (Gentry 1990).

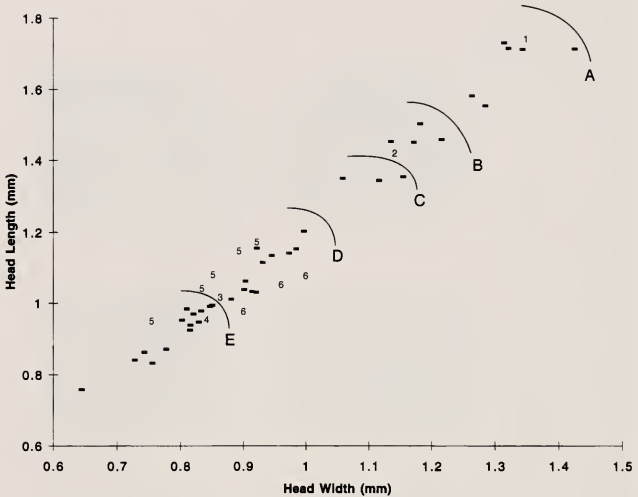Parapatric boundaries between diagnos-

Fig. 9. Worker head width vs. head length. For definitions of measurements see Figure 2. Each measurement is from a different colony, from among the largest workers in the collection. Most are from queen-associated collections, and so identification is relatively secure. Because of worker polymorphism, and inter-colony variation in the size of largest workers, the spread of points within species is large, and species generally converge in the lower left region of the plot. The curved lines delimit the maximum sizes observed for species or sets of species. A) *beltii*; B) JTL-003; C) JTL-002; D) *pittieri* complex; E) JTL-007. Numbers refer to measurements of individual workers. 1) *beltii* type; 2) *stolli* type; 3) *pittieri* type; 4) *emarginatisquamis* type; 5) *longiceps* type; 6) JTL-001. Note that *longiceps* workers tend to have relatively narrower heads, and JTL-001 workers tend to have relatively wider heads.

able groups are commonplace, and are the subject of extensive study on hybrid zones and clines (e.g. Endler 1977, Harrison & Rand 1989). In many cases they have been demonstrated to be genetically leaky boundaries, maintained by opposing forces of dispersal and selection or a number of other mechanisms (Hewitt 1989). It is common to treat such cases as intraspecific genetic structuring of a single "polytypic" species, partly due to the biological species concept and its emphasis on reproductive isolation (Cracraft 1989). Cracraft criticizes this approach on the grounds that it obscures or ignores data on differentiation, and that such differentiation data can be used to support hypotheses about the phylogenetic history of the group. Cracraft defines a phylogenetic species as "an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." In some well-sampled and well-studied groups, this approach has led to a greater understanding of biological diver-
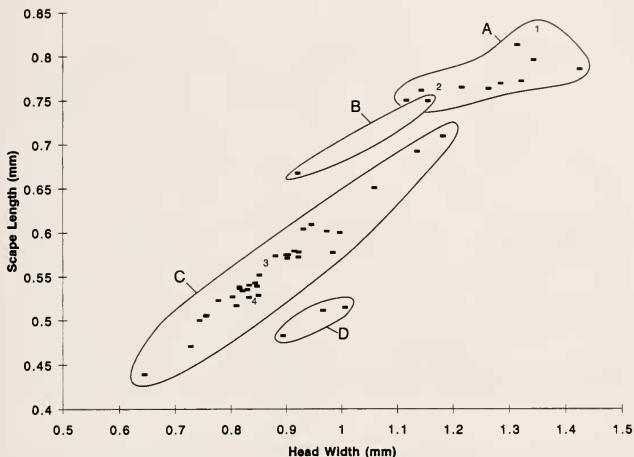
Fig. 10. Worker head width vs. scape length. Letters refer to clusters of measurements. Numbers refer to measurements of individual workers. A) *beltii*; B) JTL-002; C) *longiceps, pittieri* complex, JTL-003, JTL-007; D) JTL-001; 1) *beltii* type; 2) *stolli* type; 3) *pittieri* type; 4) *emarginatisquamis* type.

sity and an improved species-level nomenclature (e.g. Hillis 1988 for the *Rana pipiens* complex, Ward 1993 for the *Pseudomyrmex ferrugineus* complex).

However, applying a phylogenetic species concept is premature in situations like the *A. pittieri* complex, where there are data on differentiation, but they are insufficient to identify monophyletic groups. The phylogenetic species concept may not even be appropriate if the character discontinuity is a purely local phenomenon generated by strong selection or other contemporary mechanisms, in which case the differentiation is not due to a history of lineage splitting and subsequent divergence. To address this level of uncertainty regarding species boundaries, I have referred to species complexes rather than polytypic species. The observed character

discontinuities are not "captured" in any official nomenclature, but use of the term "complex" will alert a user to the presence of complex character patterns within the group, and the possibility of future resolution into multiple phylogenetic species.

A phylogenetic species concept requires autapomorphies for species. Adherence to this approach should result in greater caution being applied to the naming of new species and the matching of local species to types from distant localities. In the case of Costa Rican *Azteca*, local species are defined phenetically, as clouds of points in a metric character space. Queens from surrounding countries are often very similar to one of the Costa Rican species, but not exactly the same. As additional queens from other areas are measured and added to figure 2, the plot gradually fills in. The

A   **B**   **C**
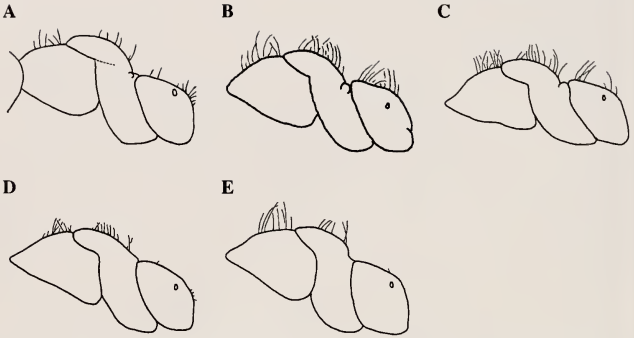
D   **E**

Fig. 11. Worker lateral mesosoma, showing dorsal pilosity. *beltii* (drawn from type. JTL-003 is similar). B. *pittieri* complex from Pacific slope near Monteverde (*longiceps* and JTL-007 are similar). C. *pittieri* complex from La Selva. D. JTL-002. E. JTL-001.

phenetic clouds of points drift around geographically. When a queen from a distant locality falls within one of the Costa Rican phenetic clouds, it is uncertain whether this is due to shared ancestry or convergence on that morphometric point. For example, *A. pittieri* complex queens from above 500m near Monteverde are very similar to the type of *A. patruelis* from Mexico. However, the ventral setae on the petiole are not exactly the same. Perhaps molecular markers or newly discovered morphological traits will reveal that the Monteverde population of *A. pittieri* and Mexican *A. patruelis* form a monophyletic group. However, I think it just as likely that there is a complex mosaic of species between Costa Rica and Mexico, and the similarity is purely coincidental (or parallel response to similar selection). In other words, even though Monteverde *A. pittieri* and Mexican *A. patruelis* are phenetically very similar, there are no well-supported synapomorphies uniting them. For these reasons, I have often relied on unavailable code names for locally-defined species,

pending larger character sets and placement in a global context.

Further understanding of Costa Rican *Azteca* will require population samples from additional localities within the country. To understand the stem-nesting *Azteca* at a global level will require similarly thorough sampling throughout the Neotropics. The lack of similar specimen coverage from other parts of the Neotropics is a severe impediment to global definitions of species.

Possible Determinants of Character Distribution in *A. pittieri* Complex

What mechanisms might produce the patterns of character variation seen in the *A. pittieri* complex? Possibilities include contemporary selection pressures and secondary contact following anthropogenic landscape changes.

Stabilizing selection may vary geographically, producing geographic variation in the presence of gene flow (Endler 1977). Selection may be strong, for the reasons noted above, increasing the likeli-

Fig. 12. Map of Costa Rica, showing localities appearing in text. Dotted line is approximate divide between Atlantic and Pacific drainages. Atlantic lowlands and southern Pacific lowlands are evergreen wet habitats with dominant South American affinities; northern Pacific lowlands are seasonal dry habitats, with dominant Mesoamerican affinities. C = Carara. P = Palmar Norte on the Río Grande de Térraba. S = Santiago de Puriscal. Buenos Aires is in the Valle del General. Bar below Monteverde is location of elevational transect.

hood that queen morphology would closely track geographic variation in selection regime. Selection gradients can produce discontinuous character variation such as that seen below Monteverde (Endler 1977). There may be a selective trade-off affecting queen size. Smaller queens would be less costly in terms of resources and could disperse farther. Larger queens with greater muscle mass in the head would have larger and more powerful mandibles for chewing into *C. alliodora*

nodes. Montane plants subject to cool, windy conditions often have thick, gnarled stems, reflecting a greater investment in structure (Lawton 1984). *Cordia alliodora* at higher elevations may thus have relatively thicker-walled nodes than at lower elevations, which would tip the selection balance in favor of relatively larger queens.

An alternative explanation is secondary contact and intergradation of previously isolated forms. Rapidly changing land use
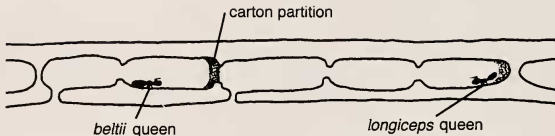
Fig. 13.   Sagittal section of *Triplaris melaenodendron* branch multiply occupied by queens of *Azteca beltii* and *longiceps*. Note that the two queens occupied chambers that were formerly continuous across perforated septa, but were subsequently separated by an asymmetrical plug of carton, with concave shaped side facing *beltii*.

in Costa Rica may be causing dramatic changes in distribution and dispersal of *C. alliodora* ants (and possibly also creating new and shifting selective regimes). In recent decades the Atlantic lowlands have gone from nearly unbroken rainforest to a largely agricultural landscape. It is unknown what the prehistoric distribution of *C. alliodora* was, but currently it is a very common pasture tree. It is a candidate species for plantation forestry, and there are several plots of various ages at La Selva. The La Selva *A. pittieri* exhibit high variance, ranging from relatively small queens with reduced propodeal pilosity to relatively larger queens with greater propodeal pilosity. A few queens examined from south of Limón exhibit the former condition. At La Selva, we may be witnessing a dynamic invasion and/or hybridization process as formerly Pacific slope forms spread with agricultural development and come into contact with Atlantic lowland rainforest forms. Prior to extensive land clearing, there may have been allopatric populations of *C. alliodora* containing morphologically differentiated populations of the *A. pittieri* complex. *Cordia alliodora* requires bare ground and high insolation to establish (J. Haggar, pers. comm.). On the Atlantic slope, trees may have been restricted to highly dynamic river margins where rivers meandered across the coastal plane. Queens with relatively short, wide heads and reduced propodeal pilosity may represent the original Atlantic lowland form, and thus

should be widespread and associated with large areas of primary forest. The mid-elevation Pacific slope form with larger head and greater propodeal pilosity may have dispersed eastward with land-clearing, or been transported with nursery stock, and may occur as pockets of invasion or else closely associated with extensive land-clearing.

The Role of Local Faunas

The above discussion illustrates some of the differences between locally and globally defined species. Sorting local species can often be done simply and quickly, using highly accessible characters. The task of global revisions is a much greater challenge, requiring large specimen bases and the use of different character systems, often those requiring dissection or molecular analysis. Ideally, large effort should go to the immediate production of global revisions, from which the clarification of local faunas will be a by product. However, publication of local faunas prior to a global understanding of taxa serves several purposes. For the systematist, local faunas provide clues to characters that differentiate locally sympatric species, and these characters may be useful in global studies. Local faunas give the field collector an idea of what to expect in local communities, and the kind of sampling effort required to adequately sample a region. They also provide identification tools, which may inspire non-systematists to use the group for study, which in turn may

increase the importance of systematic study of the group. For the non-systematist, regional faunas provide a realistic assessment of diversity, and one hopes prevent the conflation of species that is so common in ecological studies of arthropods. Finally, conservation efforts in particular regions require immediate taxonomic knowledge of the fauna, and cannot wait for the painstaking global revision of groups.

ACKNOWLEDGMENTS

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